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Abstract: Initial plant diversity might control subsequent community assembly processes and plant productivity. To study these effects, we used a biodiversity experiment (Jena Experiment) with subplots of different sown diversity that were never weeded and spontaneously colonized control plots of different size (3.5 × 3.5 m, 20 × 20 m) with and without mowing in an 8-year study. On non-sown bare plots without mowing, colonizer accumulation depended on plot size resulting in a loss of diversity in large, undisturbed (unmown) control plots after initial colonization. On sown plots that were mown, species richness converged to high levels due to the accumulation of internal colonists (species belonging to the experimental pool of sown species), while initially high species richness of external colonists (species not belonging to the experimental pool) and residents (species sown on the plot) declined over time. The convergence of total species richness at higher levels was paralleled by increased taxonomic (Simpson index, QSimp), phylogenetic (QPhylo) and trait (FDQ) diversity, whereby FDQ was greatest on plots with low resident species richness after several years. Rates of change in terms of species colonization and extinction decelerated over time irrespective of resident species richness, mowing or plot size. While the contribution of residents declined and that of colonists increased, community biomass production did not change over time. The biomasses of residents and colonists were greatest at higher levels of species richness, partial QPhylo and FDQ of the respective species group, but community biomass was consistently weakly related to total species richness and diversity indices. Our study shows that in contrast to the period of succession, "mature" plant communities resulting from natural assembly processes, favouring the coexistence of multiple species and thus high biodiversity, do no longer show significant relationships between species richness and variables related to ecosystem functioning such as primary productivity.

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Convergent high diversity in naturally colonized experimental grasslands is not related to increasing productivity

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Abstract

Initial plant diversity might control subsequent community assembly processes and plant productivity. To study these effects, we used a biodiversity experiment (Jena Experiment) with subplots of different sown diversity that were never weeded and spontaneously colonized control plots of different size (3.5 × 3.5 m, 20 × 20 m) with and without mowing in an 8-year study. On non-sown bare plots without mowing, colonizer accumulation depended on plot size resulting in a loss of diversity in large, undisturbed (unmown) control plots after initial colonization. On sown plots that were mown twice per year, species richness converged to high levels due to the accumulation of internal colonists (species belonging to the experimental pool of sown species), while initially high species richness of external colonists (species not belonging to the experimental pool) and residents (species sown on the plot) declined over time. The convergence of total species richness at higher levels was paralleled by increased taxonomic (Simpson Index, Q_{Simp}), phylogenetic (Q_{Phylo}) and trait (FD_Q) diversity, whereby FD_Q was greatest on plots with low resident species richness after several years. Rates of change in terms of species colonization, extinction and community composition decelerated over time irrespective of resident species richness, mowing or plot size. While the contribution of residents declined and the contribution of colonists increased, community biomass production did not change over time. The biomasses of residents and colonists were greatest at higher levels of species richness, partial Q_{Phylo} and FD_Q of the respective species group, but community biomass was consistently weakly related to total species richness and indices of diversity. Our study shows that in contrast to the period of succession, “mature” plant communities resulting from natural assembly processes, favouring the coexistence of multiple species and thus high biodiversity, do no longer show significant relationships between species richness and variables related to ecosystem functioning such as primary productivity.

Keywords: colonization, community assembly, phylogenetic diversity, productivity, turnover, trait diversity

Introduction

The study of temporal dynamics of plant communities may help to identify the mechanisms determining community structure and diversity and its consequences for ecosystem functioning (Rees et al., 2001). Community assembly processes involve qualitative changes (i.e. in species occurrences) as well as quantitative changes (i.e. in species abundances). Rates of community change during succession often gradually decrease from rapid turnover during early stages of community assembly to a more stable compositional structure during later stages (Prach et al., 1993; Anderson, 2007). Because assembly processes result from many spatially dependent colonization and extinction events, the rate and patterns of succession may also depend on spatial factors (Glenn-Lewin et al., 1992). In this context, the theory of island biogeography (MacArthur and Wilson, 1967) may be considered a central framework related to the temporal development of plant communities. Large isolated "islands" and those with a nearby source pool of potential colonists should have a greater species richness than smaller or distant "islands" (Holt et al., 1995; Cook et al., 2005). Furthermore, extinction rates may be higher in small "islands" due demographic stochasticity and a greater risk of local extinction for small populations (Joshi et al., 2006). The probability of successful colonization is likely to decrease with increasing species richness because a greater fraction of the available species pool has already arrived.

Neutral theory (Hubbell, 2001) proposes that dispersal and demographic stochasticity are the primary mechanisms controlling assembly processes. It further assumes that all species are "functionally equivalent", resulting in local communities with temporally randomly varying species compositions if community equilibrium is achieved at equal immigration and extinction rates. From the point of view of the niche-based theory of community assembly (MacArthur and Levins, 1967), niche overlap among functionally similar species (limiting similarity) may inhibit the colonization of new species with similar resource acquisition

79 strategies more strongly than the colonization of functionally more different species (Chesson,
80 2000). Under this scenario, local species richness is predicted to saturate and local
81 communities are assumed to have similar species compositions due to deterministic assembly
82 from the species pool (Chase, 2003). It has been suggested that a trade-off between colonizing
83 abilities and traits related to competition are core to processes of succession (Tilman, 1988;
84 Picket and McDonnell, 1989). Species with high colonizing abilities will arrive faster, but
85 their persistence depends on how fast they are replaced by later-arriving species with a greater
86 competitive ability. Consequently, species diversity may also decline through time, when
87 competition results in the dominance of a limited number of species (Whitthaker 1975;
88 Mouquet et al., 2003). Competitive exclusion is more likely in stable, uniform environments,
89 while periodic population reductions through moderate disturbance and environmental
90 fluctuations may promote consistently high levels of diversity (Huston, 1979).
91 Approaches restricted to analyses of temporal changes in taxonomic (species) composition
92 largely ignore ecological differences among the involved species. More recently, it has been
93 recognized that the comparison of phylogenetic and functional trait diversity with taxonomic
94 diversity might be more insightful for separating the various mechanisms involved in
95 community assembly processes (e.g. Gerhold et al., 2013; Purschke et al., 2013). For
96 example, increasing and convergent levels of trait diversity through time would support the
97 niche-based theory of community assembly, while decreasing levels of taxonomic and trait
98 diversity may indicate weaker competitor exclusion. Because the quantification of trait
99 diversity is based on a finite set of traits, it is assumed that phylogenetic diversity may cover a
100 larger set of biologically relevant information (Webb et al., 2002). An increasing role of biotic
101 interactions during community assembly may be reflected in decreasing phylogenetic
102 relatedness among species. This is true if important functional traits are shared by species that
103 have common ancestry or if phylogeny integrates information on biotic interactions, such as

104 shared co-evolved enemies or mutualists, which is not covered by measurable functional traits
105 (Cavender-Bares et al., 2009).
106 Guo (2003) suggested in a model based on data of natural plant succession that species
107 richness–productivity relationships would change from positive via neutral to negative during
108 succession because competition and competitive exclusion would decrease species richness
109 while increasing productivity as a community "matures". In our study region, late-
110 successional vegetation is dominated by shrubs and trees, while early-successional pioneer
111 vegetation settling on open, frequently disturbed places mainly consists of annual herbaceous
112 species. Without disturbance the early-successional pioneer species are first replaced by
113 perennial herbaceous species representing a mid-successional stage before the establishment
114 of late-successional species (Whittaker, 1975). The long-term maintenance of mid-
115 successional vegetation dominated by perennial herbaceous plant species such as grasslands
116 depends on recurring moderate disturbances such as mowing or grazing (Ellenberg, 1988).
117 For natural grasslands, the validity of the positive species richness–productivity relationship
118 observed in many artificially maintained grassland biodiversity experiments has been
119 repeatedly questioned (Thompson et al., 2005). Jiang et al. (2007) argued that differences in
120 diversity–productivity relationships between immature experimental communities, where the
121 diversity gradient is artificially maintained by weeding, and more mature natural
122 communities, are attributable to differences in species abundance patterns. In natural "mature"
123 communities, it is more likely that rare species go extinct, while high productivity levels are
124 maintained through dominant, highly productive species. In an earlier sub-experiment of the
125 Jena Experiment we found that the removal of subdominant species from sown and weeded
126 communities increased total community biomass (chapter 4 in Schmidt, 2006). Thus, the
127 successional stage of the plant community may be a central factor for shifts in species
128 richness–productivity relationships. Grassland biodiversity experiments are often established

by sowing mid-successional temperate grassland species on vegetation-free spaces and the experimental diversity gradient is maintained by regular weeding. Short-term studies in such biodiversity experiments with temperate mesophilic grassland species have shown that positive relationships between sown or total species richness and community biomass production were rapidly lost after cessation of weeding within two years at the Swiss Biodepth site (Pfisterer et al, 2004) or three years in the Jena Experiment (Petermann et al., 2010). Similar results were obtained in biodiversity experiments in subalpine grasslands (Rixen et al., 2008) and salt marshes (Doherty et al., 2011). The decay of positive species richness–productivity relationships was even faster when the natural colonization of new species was amended by seed addition (Petermann et al., 2010). The effects of sowing more species on biomass production have also been investigated in applied studies of grassland restoration on ex-arable land which did not weed unsown species after sowing. Studies restricted to two levels of sown diversity ("low" and "high" diversity) have shown that sowing more species enhances average productivity (Bullock et al., 2001; Lepš et al., 2007), but that particular low-diversity mixtures may reach similar productivity levels as high-diversity mixtures (Lepš et al., 2007).

In the present study, integrated into a large biodiversity experiment (Jena Experiment; Roscher, et al. 2004), we established subplots which were never weeded after sowing, but regularly mown twice per year. In a previous analysis, encompassing the first two years after sowing (Roscher et al., 2009b), we showed that the species number of colonists and their immigration rates decreased, while their extinction rates increased with sown species richness and that total biomass production was initially positively related to sown species richness, but varied independently from total species richness of residents (sown species) plus colonists. The maturation of such unmanipulated communities could naturally lead to saturated communities with high productivity. However, it is also possible that these "maturing"

154 communities do not achieve maximum productivity because productivity is primarily
155 determined by the efficiency of carbon fixation and stand structure, i.e. leaf area index
156 (Schulze et al., 2005), and community assembly processes starting from different initial
157 compositions are not necessarily concordant with maximizing productivity. However, this has
158 not been tested so far in a biodiversity experiment where the sown diversity gradient is not
159 maintained by weeding because experimental plant communities are rarely followed for many
160 years.
161 Here, we ask how persistently the initially sown plant diversity affects community assembly
162 processes and biomass production over a period of 8 years. In addition, we used control plots
163 at the same experimental site with free plant establishment (no sowing) on originally bare soil
164 with or without mowing twice per year and of different area (small vs. large plots) to test for
165 differences in assembly processes under these conditions. We tested the following
166 hypotheses: (1) According to the Theory of Island Biogeography, non-sown large control
167 plots show higher colonizer immigration rates and lower extinction rates and accumulate
168 more species than non-sown small control plots. (2) Unmown, non-sown control plots show
169 smaller colonizer immigration and larger extinction rates than regularly mown non-sown
170 control plots due to the accumulation of competitive mid- and late-successional species. (3)
171 Rates of community change in terms of colonizer occurrences are lower and decline faster in
172 communities initially sown with greater plant diversity because communities already
173 comprise a greater fraction of more competitive mid-successional species. (4) Species
174 richness, taxonomic, phylogenetic and trait diversity in mown communities increase and
175 converge over time because communities sown with lower plant diversity accumulate species
176 due to the occupation of free niches (local immigrations > extinctions) and communities sown
177 with the highest plant diversity lose species due to the exclusion of weaker competitors and
178 fewer open niches for the colonization of new species (extinctions > local immigrations). (5)

Even over a longer study period, strong diversity–productivity relationships do not develop because assembly processes starting from different initial compositions lead to communities with similarly high diversity and productivity.

Material and methods

Experimental design

The study was part of a large biodiversity experiment established on a former agricultural field in 2002 (Jena Experiment; Roscher et al., 2004). The experimental site is located in the floodplain of the river Saale near the city of Jena (Thuringia, Germany, 50°55`N, 11°35`E, 130 m a.s.l.) with a mean annual temperature of 9.3°C and annual precipitation of 587 mm (Kluge and Müller-Westermeier, 2000). The soil is a Eutric Fluvisol. Soil texture is sandy loam in the vicinity of the river which gradually changes to silty clay with increasing distance from the river. The Jena Experiment is based on a pool of 60 species typically occurring in Central European mesophilic grasslands used as hay meadow (Arrhenatherion community; Ellenberg, 1988). These species were considered as potentially making up a complete community or ecosystem from which species would go extinct to lead to reduced systems of 1, 2, 4, 8 or 16 species. We additionally assigned the species into four functional groups: 12 legumes, 16 grasses, 20 tall herbs and 12 small herbs. The classification into functional groups was based on a cluster analysis of a literature-derived trait matrix comprising morphological traits (growth form, capacity for lateral spread by clonal growth, plant height, leaf size, depth and type of the root system), phenological traits (life cycle, seasonality of foliage, start and duration of the flowering period) and physiological characteristics (N_2 fixation) (for further details see Roscher et al., 2004). The species richness gradient was thus crossed with a gradient in the number of functional groups (from 1 to 4) with about four

204 replicates per possible species richness × functional group number combination. Mixtures
205 were created by random selection of species with replacement. In addition, four replicates of
206 mixtures with all 60 experimental species were established resulting in a total of 82 plots of
207 20 × 20 m size. The experimental site was arranged in four blocks parallel to the riverside in
208 order to account for the gradient in soil characteristics; diversity treatments were equally
209 assigned to the blocks. Plots were sown with a total density of 1000 viable seeds per m^2, i.e.
210 seed numbers were adjusted according to germination tests under standardized conditions in
211 the laboratory. Mixtures were sown with equal numbers of viable seeds per species (for
212 details see Roscher et al., 2004). A subplot of 2.00 × 2.25 m size in each large plot was
213 permanently marked and never weeded after sowing (Roscher et al., 2009b). Plots were
214 managed by mowing and removing the mown plant material twice per year (early June,
215 September) as usual for extensively managed hay meadows in the region. Plots did not
216 receive any fertilizer. Furthermore, we used four large (20 × 20 m size) and eight small (3.5 ×
217 3.5 m size) plots within the Jena Experiment which did not receive a seed mixture but were
218 open to spontaneous colonization (= control plots). Of these plots, two large and four small
219 plots (one in each experimental block) were never mown (= unmown control plots) and the
220 others were regularly mown at the same time as the plots of the biodiversity experiment (=
221 mown control plots). All plots were surrounded by a frequently mown lawn sown with grass
222 species not belonging to the experimental species pool (for details see Roscher et al. 2004).
223
224 **Sampling**
225 Species identities and cover were visually estimated with a decimal scale (Londo, 1976) on
226 the 2.00 × 2.25 m subplots twice per year shortly before biomass harvests. Two neighbouring
227 subplots of 2.00 × 2.25 m size were surveyed in large control plots to study the same area as
228 in the small control plots (central 3 × 3 m = 9 m^2). To get reliable data on short-lived spring or

annual plants, all plots were checked for additional non-experimental species in early April (start of the growing season) and July (re-growth after first mowing). Species initially sown into a particular plot were considered resident species. All species not initially sown into a particular plot were considered colonizing species. Colonizing species were categorized as internal colonists (belonging to the 60 experimental species) or external colonists (not included in the experimental species pool). Species inventories were combined for each year to derive total species richness and maximum cover abundances of each species per subplot.

Aboveground plant biomass was harvested twice a year except in 2008, at estimated peak biomass immediately before mowing in all regularly mown large plots (late May and August). Plant material was clipped 3 cm above soil surface in a randomly placed rectangle (20 × 50 cm) in the never-weeded subplot. Plant material was sorted into residents and colonists and dried to constant weight (70°C, 48 h). Biomass data of both harvests were summed to get annual biomass production.

Trait and phylogenetic data

Trait information was assembled for all plant species recorded in the plots (203 species in total including the sown species) using published floras (Rothmaler, 2002), databases (LEDA: Kleyer et al., 2008; BiolFlor: Klotz et al., 2003) and further literature (se Supplementary Material, Appendix A.1). The set of traits comprised six traits related to growth and competitive ability and six traits related to life history (Table 1). Specific leaf area for species for which no data were available from published sources was determined from leaf samples collected at the field site or in surrounding habitats in 2009.

The phylogeny was extracted from a dated, ultrametric supertree for 4685 Central European vascular plant species (*Daphne 1.0*, Durka and Michalski, 2012) using the library *ape* (Paradis et al., 2004) in the statistical software R3.1.1 (R Development Core Team, http://www.R-

project.org). Blomberg`s K statistic (Blomberg et al., 2003) was used to evaluate the extent to which phylogenetic relatedness between species is reflected in the chosen traits using the R library *phytools* (Revell, 2012). K values close to zero indicate less phylogenetic signal than expected from a Brownian motion model of trait evolution (Blomberg et al., 2003) and imply that closely related species are functionally distinct. The significance of the phylogenetic signal was tested by comparing the observed summed absolute node contrast values (K) to a null distribution of K values based on 1000 randomizations (Revell, 2012).

Diversity indices

Rao`s quadratic diversity (Rao`s Q; Rao, 1982) expresses the average difference between two species as

$$Rao`sQ = \sum_{i=1}^{S}\sum_{j=1}^{S} p_i p_j d_{ij} \quad (1),$$

where d_{ij} is the distance between the i-th and j-th species, p_i and p_j are their relative abundances, and S is the number of species in a community. Rao`s Q can be applied to trait and phylogenetic data and is closely related to taxonomic diversity quantified as the Simpson index D being $\sum_{i}^{S} p_i^{\,2}$, thus providing a statistical framework for comparing different aspects of diversity based on trait or phylogenetic differences among species or species composition (Pavoine and Bonsall, 2011). Trait diversity (FD_Q) was calculated from the literature-based trait matrix (see Table 1). If necessary, trait data (specific leaf area, seed-bank longevity, seed mass, growth height) were log-transformed to achieve normal distribution. In case of missing data (Table 1), the mode, i.e. the most commonly occurring value across all species was used. Calculations were based on standardized trait data (mean = 0, variance = 1) and a Gower distance matrix to account for different data types (continuous, ordinal) (Pavoine et al., 2009). A phylogenetic cophenetic distance matrix derived from the phylogenetic tree (using the R

library *ape*; Paradis et al., 2004) was used for calculating phylogenetic diversity (Q_{Phylo}). FD_Q and Q_{Phylo} were weighted by annual maximum abundances for (1) all species present in a community, i.e. residents and colonists, and partitioned into (2) residents, (3) colonists and (4) dissimilarity between residents and colonists (= residents-colonists dissimilarity). In addition, taxonomic diversity as Simpson index (Q_{Simp}) based on species abundances was computed.

Data analysis

Rates of community change in colonizer and resident species occurrences per year were calculated as year-to-year species extinction rates ER = 2E/(S1+S2), immigration rates IR = 2I/(S1+S2) and species turnover TR = (E+I)/(S1+S2), where E is the number of extinctions from the previous year to the year under consideration, I is the number of immigrations from the previous year to the year under consideration, and S1 and S2 are the numbers of observed species in the respective years (Nilsson and Nilsson, 1982).

All response variables were analysed with linear mixed-effects models using the R library *nlme* (Pinheiro et al., 2009). Starting from a constant null model with plot identity nested in block as random effects, the sequence of the step-wise added fixed effects was chosen following the a priori hypotheses of the Jena Experimental design: in all analyses along the sown diversity gradient (including non-sown large mown control plots), a contrast for spontaneously colonized vs. sown communities was fitted before entering sown species richness (as a log-linear term) and functional group number (as a linear term). Afterwards, year was entered as linear variable followed by interaction terms with the previously mentioned experimental factors to test for directional changes over time. The maximum likelihood method was applied and likelihood ratio tests (L ratios) were used to assess the statistical significance of model improvement. In separate analyses of control plots, mowing type (mown vs. unmown), plot size (large vs. small) and their interactions were entered as

fixed effects.

To evaluate whether assembly processes led to a convergence in community characteristics over time, the coefficient of variation (CV) was calculated for each study year across plots sown with different plant diversity. Linear regressions of standardized variables (corrected for block-effects) were used to explore the effects of total species richness, taxonomic, phylogenetic and trait diversity on community biomass production for each study year. The respective standardized variables were used to assess their relevance for the biomass production of residents and colonists. The R library *relaimpo* (Grömping, 2006) was used for assessing the relative importance of different predictor variables defined as the R^2 contribution averaged over orderings among regressors (Grömping, 2007).

Results

Spontaneous colonization in non-sown control plots

On average, colonizer species richness on a standardized sampling area of 9 m^2 was higher in small than in large control plots, but effects of plot size differed between mown and unmown control plots (Fig. 1a; Table 2). After a strong increase in species richness during initial settlement in the first two years, separate analyses (not shown) indicated that large mown control plots gradually accumulated more species, while large unmown control plots lost species from the third year onwards. Richness of colonizing species fluctuated at higher levels in small control plots irrespective of mowing. Species richness of internal colonists was higher, and species richness of external colonists was lower in mown than in unmown control plots (Fig. 1b–c; Table 2). The temporal accumulation of internal colonists differed between mown and unmown control plots and plot sizes: mown (large and small control plots) > unmown (small control plots) > unmown (large control plots). After an initial increase from

the first to the second year, species richness of external colonists decreased continuously over time (Fig. 1c). Year-to-year changes in colonizer occurrences did not depend on mowing type and size of the spontaneously colonized control plots (Fig. 1d-f, Table 2). Year-to-year changes in colonizer immigration and turnover rates declined over time, while colonizer extinction rates did not show directional temporal changes, but fluctuated among years (Table 2). Temporal changes in colonizer extinction and turnover rates were greater in large than in small control plots irrespective of mowing.

Taxonomic diversity (Q_{Simp}) and phylogenetic diversity (Q_{Phylo}) of colonists did not differ between mown and unmown control plots, but were higher in small than in large control plots (Fig. 1g, h; Table 2). Trait diversity (FD_Q) of colonists was higher in mown than in unmown control plots (Fig. 1i; Table 2). Plot size effects on FD_Q depended on mowing type: FD_Q was higher in small than in large unmown control plots, but did not differ between small and large mown control plots. After an initial increase from the first to the second year of the experiment, Q_{Simp}, Q_{Phylo} and FD_Q declined through time in large unmown control plots. FD_Q also declined in small unmown control plots, while FD_Q in mown control plots fluctuated at higher levels over time. Irrespective of mowing Q_{Simp} and Q_{Phylo} had constantly high levels in small control plots, while similar high levels were reached after several years in large mown control plots.

Spontaneous colonization in plots of varying initially sown plant diversity

Effects of sown plant diversity on total species richness

Overall, total species richness (total of residents and colonists) did not differ between unsown mown control plots and sown (mown) plots, but increased with sown species richness as expected by design (Fig. 2a; Table 3). Total species richness generally increased through

353 time. Species gain over time became smaller with increased sown plant diversity, and species
354 richness in communities initially sown with 60 species decreased over time. Resident species
355 richness decreased slightly through time, which was mainly due to a loss of species in
356 communities sown with higher plant diversity (Fig. 2b). Nevertheless, communities with
357 higher sown species richness retained greater resident species richness than communities with
358 low sown species richness. Species richness of colonists decreased with higher sown species
359 richness (Fig. 2c; Table 3). The overall gain of colonists through time was fastest on plots
360 with low sown species richness and functional group number. Opposing temporal trends
361 emerged for internal and external colonists. While species richness of external colonists
362 decreased, species richness of internal colonists increased through time (Table 3; Fig. 2d, e).
363 The enhanced colonization of internals in communities with lower sown plant diversity
364 increased through time, while effects of sown plant diversity on species richness of external
365 colonists did not change over time (Table 3). Total and colonizer species richness converged
366 among plots sown with different plant diversity over time (decreasing coefficient of
367 variation), while differences in resident species richness were maintained (Fig. A.1).
368
369 *Effects of sown plant diversity on rates of community change*
370 Immigration, extinction and turnover rates of resident species increased with sown species
371 richness. On average extinction rates of residents increased and immigration and turnover
372 rates of residents decreased through time (analyses not shown). Immigration, extinction and
373 turnover rates of colonists did not differ between non-sown plots and plots established
374 through sowing (Table 3). Colonizer extinction rates increased and colonizer immigration
375 rates decreased with sown species richness. Colonizer immigration, extinction and turnover
376 rates decreased through time (Fig. 3b-d; Table 3). Effects of sown species richness on

377 colonizer immigration and extinction rates declined through time (significant interaction Y ×
378 sown SR; Table 3).
379
380 *Effects of sown plant diversity on taxonomic, trait and phylogenetic diversity*
381 Blomberg`s K values were below 1 in all considered traits with the exception of the species`
382 ability for symbiotic N_2 fixation and growth height (Table A.1). However, all traits apart from
383 life form, duration of flowering and type of reproduction had K values that were greater than
384 expected by chance indicating a low, but significant phylogenetic signal.
385 Taxonomic diversity (Q_{Simp}) and phylogenetic diversity (Q_{Phylo}) increased with sown species
386 richness, while trait diversity (FD_Q) did not depend on sown species richness (Table 4). On
387 average, Q_{Simp}, Q_{Phylo} and FD_Q increased through time (Table 4; Fig. 4a, c, e). This increase
388 over time was more pronounced in communities with a lower sown plant diversity resulting in
389 increased convergence of Q_{Simp} and Q_{Phylo} among communities (Fig. A.2a). In contrast, the
390 initially high levels of FD_Q in communities sown with high species richness were exceeded by
391 higher levels of FD_Q in communities sown with a low species richness in later years (Fig. 4e).
392 However, communities also became more similar in FD_Q through time (Fig. A.2a).
393 Partial Q_{Simp} of residents decreased with sown plant diversity in communities with 1 to 16
394 sown species, while communities with 60 sown species had the highest levels of residents`
395 Q_{Simp} (Fig. A.3a). In contrast, partial Q_{Phylo} and FD_Q of residents increased with sown plant
396 diversity (Fig. A.3c, e). Partial Q_{Simp}, Q_{Phylo} and FD_Q of residents decreased through time in
397 plant communities with 1 to 16 sown species, but remained large in communities with 60
398 sown species resulting in a divergence among communities through time (Fig. A.2b; Table 4).
399 Partial Q_{Simp}, Q_{Phylo} and FD_Q of colonists increased through time (Fig. A.3b, d, f). This
400 increase was more pronounced in communities with lower sown species richness leading to a
401 convergence among communities (Fig. A.2c). Taxonomic, phylogenetic and trait

dissimilarities between residents and colonists declined strongly from the first to the second study year, in particular at higher sown species richness. In later years, taxonomic, phylogenetic and trait dissimilarities between residents and colonists decreased in communities with one, two or four initially sown species, while they increased in communities with eight and 16 initially sown species and were close to zero in communities initially sown with 60 species (Fig. 4b, d, f).

Effects of sown plant diversity on biomass production

Community biomass production did not differ between spontaneously colonized mown control plots and sown (mown) plots. On average, community biomass increased with sown species richness. Biomass production fluctuated among study years, but did not show directed temporal trends (Fig. 5a; Table 3). Resident biomass production also increased with sown species richness, but the biomass of residents declined through time. This decline was more pronounced in communities sown with lower plant diversity (Fig. 5b; Table 3). In contrast, biomass production of colonists decreased with increased sown species richness. Colonists increased their biomass production and effects of initial sown species richness on biomass of colonists became weaker over time (Fig. 5c; Table 3). After productivity levels across communities diverged during the initial five years of the experiment, biomass production was more similar among communities in later years (Fig. A.2a). In contrast, resident biomass diverged and the biomass of colonists converged among communities over time (Fig. A.2b, c).

Disappearance of diversity–productivity relationships during community regeneration

Diversity-related predictor variables explained a significant proportion of variation in community biomass production (with the exception of 2004 (year 3), 2007 (year 6)), but the

427 proportion of explained variation was small in all study years (between 7–23%). While FD_Q
428 was the most important predictor positively related to community biomass production from
429 2004 to 2006 (year 3–5), the relationship between FD_Q and community biomass production
430 became weaker and even negative in the last study year (Fig. 6a). The relative importance of
431 SR_{real}, Q_{Phylo} and Q_{Simp} in explaining community biomass production varied over time (Table
432 A.3).
433 Partial diversity-related predictors explained a greater, but annually variable proportion of
434 variation in biomass production of colonists (41–63%), while the proportion of explained
435 variation in biomass production of residents (19–77%) increased over time. The relative
436 importance of partial resident SR_{real}, Q_{Simp}, Q_{Phylo} and FD_Q was similar in explaining resident
437 biomass production (Fig. 6b). In contrast, partial colonizer SR_{real} had a smaller relative
438 importance in explaining colonizer biomass production than partial colonizer Q_{Simp}, Q_{Phylo} and
439 FD_Q (Fig. 6c).
440

441 ## Discussion

442

443 **Rates of community change and species richness**

444 Rates of community change in terms of colonizer occurrences generally decelerated through
445 time. Decreasing species immigration and turnover rates are typical for succession and may
446 be ascribed to increasing competitive interactions and a decreasing pool of potential new
447 colonists (Anderson, 2007). Consistent with the concept of initial floristic composition (Egler,
448 1954) immigration rates were largest in the early phase of colonization and decreased sharply
449 from the second to the third year in non-sown control plots. Relative to immigration rates,
450 extinction rates have been shown to be low and to have less consistent temporal patterns
451 during succession (Anderson, 2007). Indeed, extinction rates in unsown control plots

fluctuated over time. Based on the framework of the Theory of Island Biogeography, we hypothesized that large non-sown control plots show larger colonizer immigration rates and lower extinction rates than non-sown small control plots (hypothesis 1). Contrary to our expectation and to earlier studies such as Joshi et al. (2006), colonizer immigration and extinction rates did not depend on plot size. Cook et al. (2005) reported from a succession study in experimentally fragmented patches that ”island” size did not show consistent effects on species richness in the first 12 years, but greater richness on large “islands” developed after this period. Furthermore, previous studies have pointed out that patch size effects might be dependent on the isolation of the “islands” (Holt et al., 1995). In our study “islands” were embedded in a matrix of neighbouring plots, which served as a source pool for internal colonists. Thus, higher average numbers of colonizer species on small plots could indicate greater edge effects. However, in later years more species were assembled on the same sampling area in large mown than in small mown control plots suggesting negative effects of small fragmented patches (Fahrig et al., 2003).

Contrary to our expectation, rates of community change on non-sown control plots did not generally depend on disturbance by mowing (hypothesis 2), but depended on plot size. In line with our expectation, species richness decreased in large unmown control plots after initial colonization, while this process started in later years in small unmown control plots (Fig. 1a). The accelerated loss of species in large unmown plots is most likely due to the accumulation of biomass and thereby increasing light competition, which limits species diversity at small spatial scale in highly productive habitats (Huston, 1979). In contrast, it is likely that larger edge effects slowed down this process in small unmown control plots.

Immigration rates of colonists were lower and their extinction rates were higher at high sown plant diversity, which is consistent with a previous study carried out shortly after the establishment of our experiment (Roscher et al., 2009b). These results are in line with

hypothesis 3, although contrary to our expectation colonizer turnover rates did not depend on sown diversity. In contrast to non-sown control plots, both colonizer immigration and extinction rates decreased continuously and moderately through time (Fig. 3a-b). Both, mown control plots and sown plots of the diversity experiment gradually accumulated a greater number of internal colonists. External colonists generally declined over time, which is in line with a study in weeded communities of the first three years of the Jena Experiment (Roscher et al., 2009a). Consistent with the view that a colonization–competition trade-off is core to succession processes (Tilman, 1988) and results from many studies of succession (Tilman, 1990), species with early-successional traits (i.e. annual life cycle, reproduction by seeds, small seeds) dominated as colonists in species-poor, newly established experimental communities, while mid-successional traits (perennial life cycle, taller growth, vegetative reproduction) characterized later colonists and those in communities sown with greater diversity (Roscher et al., 2015). Many colonists in the early years of our experiment were species typical for ruderal and arable sites (Table A.1, Fig. A.3) and were present in the soil seed bank of the experimental field. Later, internal colonists accounted for the largest proportion of colonizing species, these were typically mid-successsional grassland species more tolerant to competition (Fig. 2d). The consistently negative relationship between colonizer species richness and sown initial plant diversity, which was evident even after eight years, was probably due to the greater stability of the resident communities when sown with a larger number of mid-successional grassland species (Roscher et al., 2013). Nevertheless, over time we found a gradual accumulation of species in communities sown with 1–16 species, which was weaker in plant communities initially sown with higher species richness, suggesting that more open niches were available in these communities. Saturating levels of species richness through species accumulation are often observed in secondary succession (Tilman, 2004). Communities sown with all experimental species, however, gradually lost

502 species resulting in converging levels of species richness over time (Fig. A.2a).

503

504 **Taxonomic, phylogenetic and trait diversity**

505 Experiments with artificially assembled plant communities have shown that the colonization
506 of functionally similar species is more likely to be suppressed compared with the colonization
507 of functionally more different species, but so far these analyses have mostly been performed
508 on a functional-group level or have focussed on single species (e.g. Fargione et al., 2003;
509 Mwangi et al., 2007; Hooper and Dukes, 2010; Petermann et al., 2010). In the present study,
510 Rao`s Q was applied as a continuous measure of trait diversity (FD_Q) and partitioned into the
511 contribution of residents, colonists and residents–colonists dissimilarity. Supporting our initial
512 hypothesis 4, FD_Q increased over time in all mown plots. In contrast, FD_Q declined after an
513 initial increase in unmown control plots. Thus, non-random assembly processes increased
514 functional dissimilarity and the chance for complementarity among species, which is in line
515 with previous analyses at the functional-group level. At the highest level of initially sown
516 species richness, however, FD_Q decreased after several years suggesting that declining species
517 richness at the highest level of productivity was due to the exclusion of weaker competitors
518 and that differences in competitive ability resulted in trait convergence (Grime, 2006; Isbell et
519 al, 2009). In spite of the remarkable stability of residents regarding their species richness,
520 partial FD_Q of residents declined in contrast to an increasing partial FD_Q of colonists. Thus,
521 colonists did not simply occupy “empty niche space”, but increasingly constrained the niche
522 space of residents. In line with the increased niche occupation by colonists, residents–
523 colonists trait dissimilarity decreased over time in communities initially sown as
524 monocultures or two-species mixtures. In contrast, trait dissimilarity between residents and
525 colonists increased over time with higher sown species richness, supporting the idea that
526 species are most likely to coexist if they are functionally different.

Phylogenetic diversity (Q_{Phylo}) also increased over time and converged at high levels, which is in accordance with studies in biodiversity experiments in which weeding was stopped after several years (Cadotte and Strauss, 2011; Allan et al., 2013). The initial decline in communities with lower sown species richness was mainly due to a decrease in partial Q_{Phylo} of colonists and suggested that the success of early colonists was controlled by interspecific differences that were not covered by our trait matrix (Mayfield and Levine, 2010). Although FD_Q and Q_{Phylo} showed parallel temporal trends, which can be expected given that most traits showed phylogenetic conservatism (Table A.1), Q_{Phylo} did not decrease after several years at high levels of sown species richness as observed in FD_Q. These results support the notion that traits and phylogeny may provide complementary information on species differences (Cadotte et al., 2013), i.e. species being similar in traits considered in FD_Q possess additional phylogenetically conserved features that are important for their coexistence.

Diversity–productivity relationships

Strong diversity–productivity relationships are found if species are deliberately removed from intact ecosystems. This is the basic idea of all biodiversity–ecosystem functioning experiments, which simulate random species extinction by assembling communities with reduced numbers of species (Schmid and Hector, 2004). In the present study we allowed the experimentally reduced ecosystems to regenerate by admitting the experimentally extinguished species to colonize. Our hypothesis was that the regenerated systems would not show any strong diversity–productivity relationships because assembly processes starting from different initial compositions would lead to similarly high diversity and productivity (hypothesis 5). Varying diversity–productivity relationships may potentially be explained by the reduced importance of positive selection and complementarity effects and a greater importance of competitive exclusion in more “mature” natural communities (Jiang et al.,

552 2009). In our experiment, we found evidence for competitive exclusion in mixtures initially
553 sown with 60 species, where total species richness as well as FD_Q declined after several years.
554 Nevertheless, these communities maintained the highest productivity in all study years
555 suggesting that at very high level a reduction of FD_Q does not result in reduced community
556 productivity. Interestingly, sown species richness as well as the realized number of resident
557 species had consistently positive effects on the biomass production of resident species (Table
558 3, Fig. 6b). This result is in line with the observed persistence of the positive relationship
559 between sown species richness and their biomass production in a grassland biodiversity
560 experiment, where weeding was stopped after several years. However, in this study colonists
561 were predominantly non-native species (Huang et al., 2013), while the colonists in our study
562 mainly consisted of native species or non-native species, which have a long history of
563 introduction in the study area (Table. A.1). In our study, the biomass production of residents
564 declined over time in communities sown with 1-16 species in parallel with a gradual decline
565 in Q_{Simp}, FD_Q and Q_{Phylo} of residents (Fig. A.2 a, e, e), while these measures of diversity as
566 well as productivity of residents remained more stable in the mixtures sown with 60 species.
567 Interestingly, FD_Q reached the highest levels when colonization started in unsown plots yet
568 these communities had low productivity throughout the study period. This is consistent with a
569 previous experiment on ex-arable fields comparing non-sown plots with sown plots of low
570 and high species richness (Lepš et al., 2007). Overall, however, partial diversity of residents
571 and colonists, were reliable predictors of biomass production of residents and colonists of the
572 respective species group, supporting the view that a greater diversity increases the chance for
573 incorporating highly productive species. This is in line with common practice in agriculturally
574 managed grasslands, where species with traits related to high biomass production are
575 favoured by sowing, while promoting the extinction of other, unwanted species.

Although total species richness was the most important predictor of positive diversity effects on productivity during the initial phase (Table A.3.), the diversity effects on community biomass production disappeared over time as the systems with reduced sown diversity were allowed to regenerate and accumulate similarly high levels of diversity as communities with higher sown diversity (Fig. 6a). Interestingly, the trajectory from a strong to a weak diversity–productivity relationship was not a smooth one. Instead, the proportion of explained variation in community biomass production and the relative importance of different predictors fluctuated between years. Most strikingly, positive effects of FD_Q on biomass production peaked in the fourth year after sowing, but declined afterwards to even negative relationships between FD_Q and biomass production. Thus, other aspects of community composition also affect community productivity in the longer term and should be considered in future studies.

Conclusions

The aim of our study was to test the regeneration potential of plant communities after local extinction events have reduced their diversity to different numbers and compositions of species. We show that community assembly processes during recovery from the local species pool are not random, but result in increased and convergent levels of phylogenetic diversity, while trait diversity is limited through competitive exclusion at high levels of sown species richness (Fig. 7). Convergent high levels of species richness, phylogenetic and trait diversity among the communities are not associated with maximum community productivity suggesting that “maturation” of the communities starting regeneration from different initial compositions does not maximize productivity.

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604

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758 Table 1: List of functional traits used in analyses compiled from different sources (BiolFlor:
759 Klotz et al., 2003; LEDA: Kleyer et al., 2008; Rothmaler, 2002; own measurements) and their
760 completeness (i.e. proportion of species for which trait data were available)

Variable	Type of variable	Completeness
Traits related to growth		
Growth height	continuous (m)	100%
Specific leaf area	continuous (mm^2_{leaf} mg^{-1}_{leaf})	97%
Root type	binary (0 = no taproot, 1 = taproot)	100%
N_2 fixation	binary (0 = non, 1 = yes)	100%
Growth form	ordinal (1 = rosulate; 2 = semirosulate; 3 = without basal leaf rosette)	100%
Life form	ordinal (1 = annual; 2 = biennial or monocarpic perennial; 3 = perennial)	100%
Traits related to life-history		
Start of flowering period	ordinal (1 = before May; 2 = May; 3 = June; 4 = July)	99%
Duration of flowering period	ordinal (1 = two months or less; 2 = three months; 3 = four months; 4 = more than 4 months)	99%
Age of first flowering	ordinal (1 = less than 1 year; 2 = between 1-5 years, 3 = more than 5 years)	91%
Seed mass	continuous (mg)	94%
Seed bank longevity	continuous (between 0 and 1)	96%
Type of reproduction	ordinal (1 = by seed; 2 = mostly by seed, rarely vegetative; 3 = by seed and vegetative; 4 = mostly vegetative)	100%

761

762 Table 2: Mixed-effects model analyses of colonizer species richness (and partitioned into
763 internal and external colonists), colonizer immigration, extinction and turnover rates between
764 subsequent years, and taxonomic diversity (Q_{Simp}), phylogenetic diversity (Q_{Phylo}) and trait
765 diversity (FD_Q) based on cover abundances (2002-2009) in spontaneously colonized control
766 plots of different sizes either regularly mown or unmown.

Source of variation	Total colonizer species richness		Internal colonizer species richness		External colonizer species richness	
	L ratio	p	L ratio	p	L ratio	p
Unmown vs. mown (M)	2.49	0.115	13.47	<0.001 ↑	4.21	0.040 ↓
Plot size (S)	5.20	0.023 ↓	4.73	0.030 ↓	2.15	0.142
M x S	11.53	0.001	5.06	0.025	5.28	0.022
Year (linear)	6.29	0.012 ↑	74.57	<0.001 ↑	24.18	<0.001 ↓
Year x M	4.69	0.030	52.42	<0.001	4.61	0.032
Year x S	0.22	0.641	0.01	0.931	0.33	0.567
Year x M x S	6.29	0.012	17.29	<0.001	0.85	0.356
Source of variation	Colonizer immigration rate		Colonizer extinction rate		Colonizer turnover rate	
	L ratio	p	L ratio	p	L ratio	p
Unmown vs. mown (M)	1.74	0.188	0.46	0.498	<0.01	0.984
Plot size (S)	0.04	0.837	0.34	0.560	0.25	0.615
M x S	0.53	0.468	2.16	0.142	0.19	0.660
Year (linear)	46.75	<0.001 ↓	0.32	0.574	65.02	<0.001 ↓
Year x M	1.39	0.239	0.04	0.836	1.68	0.194
Year x S	0.92	0.337	4.64	0.031	6.47	0.011
Year x M x S	<0.01	0.965	0.84	0.360	0.03	0.864
Source of variation	Colonizer Q_{Simp}		Colonizer Q_{Phylo}		Colonizer FD_Q	
	L ratio	p	L ratio	p	L ratio	p
Unmown vs. mown (M)	0.61	0.435	0.29	0.588	8.15	0.004 ↑
Plot size (S)	26.68	<0.001 ↓	12.61	<0.001 ↓	2.47	0.116
M x S	8.61	0.003	6.54	0.011	13.18	<0.001
Year (linear)	9.19	0.002 ↑	8.97	0.003 ↑	2.31	0.129
Year x M	4.51	0.034	3.84	0.050	6.54	0.011
Year x S	1.34	0.247	0.87	0.351	<0.01	0.974
Year x M x S	7.54	0.006	8.04	0.005	4.55	0.033

767 Models were fitted by stepwise inclusion of fixed effects. Listed are the results of likelihood
768 ratio tests (L ratio) that were applied to assess model improvement and the statistical
769 significance of the fixed effects (p values). Arrows indicate increase (↑) or decrease (↓) of the
770 variables with management (unmown vs. mown), plot size (small vs. large) and year of the
771 experiment.

Table 3: Mixed-effects model analyses of species richness (total, residents, colonists and colonists separated into internal and external species), colonizer immigration, extinction and turnover rates between subsequent years, and biomass production (community, residents, colonists) across experiment years (2002-2009) in large mown plots either spontaneously colonized or initially sown with different plant diversity.

Source of variation	Total species richness		Resident species richness		Total colonizer species richness		External colonizer species richness	
	L ratio	p	L ratio	p	L ratio	p	L ratio	p
Non-sown vs. sown	0.05	0.816			3.50	0.061	1.78	0.183
Sown SR (log-linear)	22.98	<0.001 ↑	370.33	<0.001 ↑	86.37	<0.001 ↓	51.94	<0.001 ↓
Sown FG (linear)	3.14	0.077	0.57	0.452	3.71	0.054	1.90	0.168
Year (linear)	146.56	<0.001 ↑	20.36	<0.001 ↓	185.26	<0.001 ↑	384.07	<0.001 ↓
Y x non-sown vs. sown	1.97	0.160			1.72	0.190	0.55	0.460
Y x Sown SR (log-linear)	165.88	<0.001	4.55	0.033	130.31	<0.001	3.13	0.077
Y x Sown FG (linear)	4.45	0.035	7.13	0.008	6.09	0.014	0.24	0.624

Source of variation	Internal colonizer species richness		Colonizer immigration rate		Colonizer extinction rate		Colonizer turnover rate	
	L ratio	p	L ratio	p	L ratio	p	L ratio	p
Non-sown vs. sown	2.44	0.118	0.02	0.892	0.82	0.365	1.32	0.251
Sown SR (log-linear)	66.01	<0.001 ↓	12.87	<0.001 ↓	4.91	0.027 ↑	2.72	0.099
Sown FG (linear)	0.25	0.617	1.21	0.271	0.02	0.902	0.92	0.337
Year (linear)	850.32	<0.001 ↑	54.45	<0.001 ↓	160.90	<0.001 ↓	257.95	<0.001 ↓
Y x non-sown vs. sown	0.10	0.756	2.65	0.104	3.38	0.066	0.06	0.809
Y x Sown SR (log-linear)	84.24	<0.001	7.72	0.006	14.67	<0.001	0.05	0.820
Y x Sown FG (linear)	9.97	0.002	1.37	0.241	3.22	0.073	0.45	0.503

Source of variation	Community biomass production		Resident biomass production		Colonizer biomass production	
	L ratio	p	L ratio	p	L ratio	p
Non-sown vs. sown	2.62	0.105			3.72	0.054
Sown SR (log-linear)	16.57	<0.001 ↑	55.66	<0.001 ↑	74.92	<0.001 ↓
Sown FG (linear)	1.00	0.318	3.53	0.060	0.54	0.461
Year (linear)	1.74	0.187	127.30	<0.001 ↓	194.65	<0.001 ↑
Y x non-sown vs. sown	0.02	0.893			5.99	0.014
Y x Sown SR (log-linear)	2.60	0.107	40.66	<0.001	3.10	0.078
Y x Sown FG (linear)	0.21	0.646	4.65	0.031	0.16	0.688

Models were fitted by stepwise inclusion of fixed effects. Listed are the results of likelihood ratio tests (L ratio) that were applied to assess model improvement and the statistical significance of the fixed effects (p values). Arrows indicate increase (↑) or decrease (↓) of the variables between non-sown and sown plots, with sown species richness (= SR), functional group number (FG) and year of the experiment (Y).

Table 4: Mixed-effects model analyses of taxonomic diversity Q_{Simp}, phylogenetic diversity Q_{Phylo} and trait diversity FD_Q across all species, separately for residents and for colonists and as residents-colonists dissimilarity based on cover abundances across experiment years (2002-2009) in large mown plots either spontaneously colonized or initially sown with different plant diversity.

Source of variation	Total Q_{Simp}		Partial resident Q_{Simp}		Partial colonizer Q_{Simp}		Between resident-colonizer Q_{Simp}	
	L ratio	p	L ratio	p	L ratio	p		
Non-sown vs. sown	0.02	0.881			8.05	0.005 ↓		
Sown SR (log-linear)	71.43	<0.001 ↑	143.79	<0.001 ↓	126.99	<0.001 ↓	3.61	0.057
Sown FG (linear)	2.22	0.136	5.55	0.019 ↓	6.15	0.013 ↓	0.74	0.390
Year (linear)	148.74	<0.001 ↑	84.20	<0.001 ↓	201.78	<0.001 ↑	6.61	0.010
Y x non-sown vs. sown	1.88	0.170			2.97	0.085		
Y x Sown SR (log-linear)	75.41	<0.001	1.04	0.307	41.87	<0.001	33.65	<0.001
Y x Sown FG (linear)	0.03	0.853	0.04	0.840	1.07	0.300	0.30	0.584
Source of variation	Total Q_{Phylo}		Partial resident Q_{Phylo}		Partial colonizer Q_{Phylo}		Between resident-colonizer Q_{Phylo}	
	L ratio	p	L ratio	p	L ratio	p	L ratio	p
Non-sown vs. sown	0.08	0.773			7.27	0.007 ↓		
Sown SR (log-linear)	53.00	<0.001 ↑	153.71	<0.001 ↑	128.66	<0.001 ↓	3.37	0.066
Sown FG (linear)	0.68	0.411	11.92	0.001 ↑	6.12	0.013 ↓	0.35	0.554
Year (linear)	139.66	<0.001 ↑	77.90	<0.001 ↓	181.70	<0.001 ↑	5.36	0.021 ↑
Y x non-sown vs. sown	1.72	0.189			2.74	0.098		
Y x Sown SR (log-linear)	53.95	<0.001	0.80	0.371	38.46	<0.001	31.95	<0.001
Y x Sown FG (linear)	4.94	0.026	0.09	0.765	1.33	0.249	0.05	0.820
Source of variation	Total FD_Q		Partial resident FD_Q		Partial colonizer FD_Q		Between resident-colonizer FD_Q	
	L ratio	p	L ratio	p	L ratio	p	L ratio	p
Non-sown vs. sown	1.21	0.271			6.77	0.009 ↓		
Sown SR (log-linear)	0.12	0.727	130.13	<0.001 ↑	127.83	<0.001 ↓	4.91	0.027 ↓
Sown FG (linear)	0.55	0.460	19.53	<0.001 ↑	7.74	0.005 ↓	0.03	0.855
Year (linear)	109.01	<0.001 ↑	64.89	<0.001 ↓	351.30	<0.001 ↑	31.20	<0.001 ↑
Y x non-sown vs. sown	5.11	0.024			1.90	0.168		
Y x Sown SR (log-linear)	82.57	<0.001	0.08	0.775	53.43	<0.001	14.01	<0.001
Y x Sown FG (linear)	13.05	<0.001	0.98	0.323	4.24	0.039	0.48	0.489

Models were fitted by stepwise inclusion of fixed effects. Listed are the results of likelihood ratio tests (L ratio) that were applied to assess model improvement and the statistical significance of the fixed effects (p values). Arrows indicate increase (↑) or decrease (↓) of the variables between non-sown and sown plots, with sown species richness (= SR), functional group number (FG) and year of the experiment (Y).

792 Figure captions

793

794 Figure 1: Colonizer species richness (a), partitioned into internal colonizer species (b), and
795 external colonizer species (c), colonizer immigration rates (d), colonizer extinction rates (e),
796 colonizer turnover rates (f), taxonomic diversity Q_{Simp} (Simpson index D) (g), phylogenetic
797 diversity Q_{Phylo} (h), and trait diversity FD_Q (i) across experiment years (2002-2009) in large
798 and small spontaneously colonized control plots (without seed addition), either mown or
799 unmown. Values are based on maximum annual species abundances from replicated
800 inventories (9 m^2) and represent arithmetic means (± 1 SE) per treatment.

801

802 Figure 2: Total species richness (a), resident species richness (b), colonizer species richness
803 (c), partitioned into internal colonists (d), and external colonists (e) across experiment years
804 (2002-2009) in large mown plots either spontaneously colonized or initially sown with
805 different levels of plant diversity. Values are based on replicated species inventories on
806 subplots of 2.00 × 2.25 m size and represent arithmetic means (± 1 SE) across all assemblages
807 per sown species-richness level.

808

809 Figure 3: Colonizer immigration rates (a), extinction rates (b), and turnover rates (c) between
810 subsequent years (from 2002-2009) in large mown plots either spontaneously colonized or
811 initially sown with different levels of species richness. Values are based on replicated species
812 inventories on subplots of 2.00 × 2.25 m size and represent arithmetic means (± 1 SE) across
813 all assemblages per sown species-richness level.

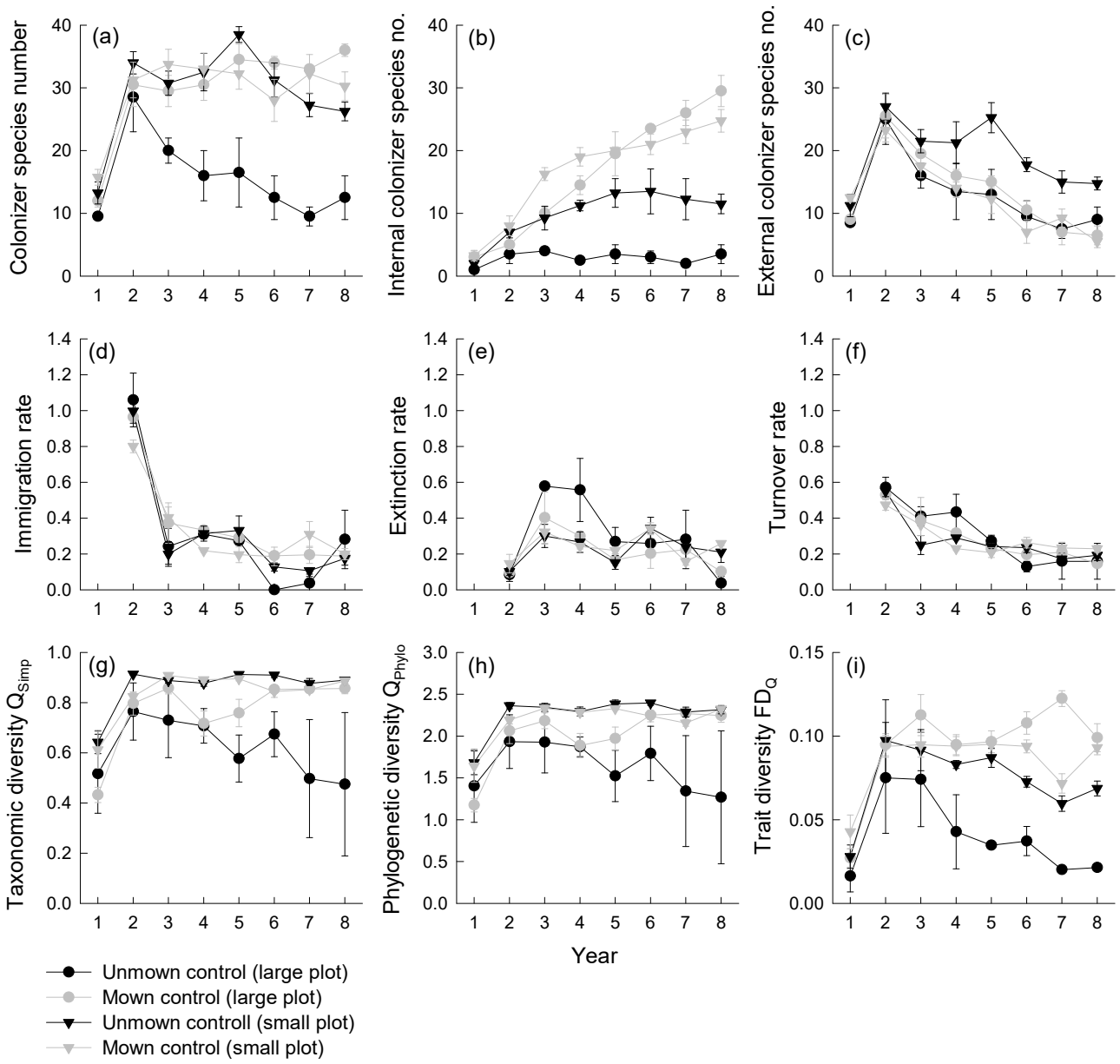
814

815 Figure 4: Taxonomic diversity Q_{Simp} (Simpson index) (a), taxonomic dissimilarity between
816 residents and colonists (b), phylogenetic diversity Q_{Phylo} (c), phylogenetic dissimilarity

817 between residents and colonists (d), trait diversity FD_Q (e), and trait dissimilarities between
818 residents and colonists (f) across experiment years (2002-2009) in large mown plots either
819 spontaneously colonized or initially sown with different levels of plant diversity. Values are
820 based on maximum species abundances from replicated inventories on subplots of 2.00 × 2.25
821 m size and represent arithmetic means (± 1 SE) across all assemblages per sown species-
822 richness level.
823
824 Figure 5: Community biomass production (a), partitioned into biomass production of residents
825 (b), and biomass production of colonists across experiment years (2003-2009) in large mown
826 plots either spontaneously colonized or initially sown with different levels of plant diversity.
827 Values represent arithmetic means (± 1 SE) across all assemblages per sown species-richness
828 level. Note that no data were available for 2008 and for large mown control plots in 2003 and
829 2004.
830
831 Figure 6: Standardized regression slopes (± 1 SE) using total species richness, taxonomic
832 diversity (Q_{Simp}), phylogenetic diversity (Q_{Phylo}) and trait diversity (FD_Q) as predictors for (a)
833 community biomass production, and the respective partial variables as predictors for (b)
834 biomass production of residents, and (c) biomass production of colonists in large mown plots
835 per experiment year.
836
837 Figure 7: Illustration of community assembly processes in naturally colonized experimental
838 grasslands sown with different diversity. The first three columns show average temporal
839 changes in species richness, trait diversity (FD_Q), phylogenetic diversity (Q_{Phylo}) and biomass
840 production differentiated into the contribution of residents and colonizers exemplarily for low
841 diversity (two sown species), medium diversity (eight sown species) and high diversity (60

842 sown species). The right column schematically summarizes convergence in total species
843 richness, FD_Q and Q_{Phylo} across low, medium and high sown diversity and associated levels of
844 biomass production through time.

845 Figure 1



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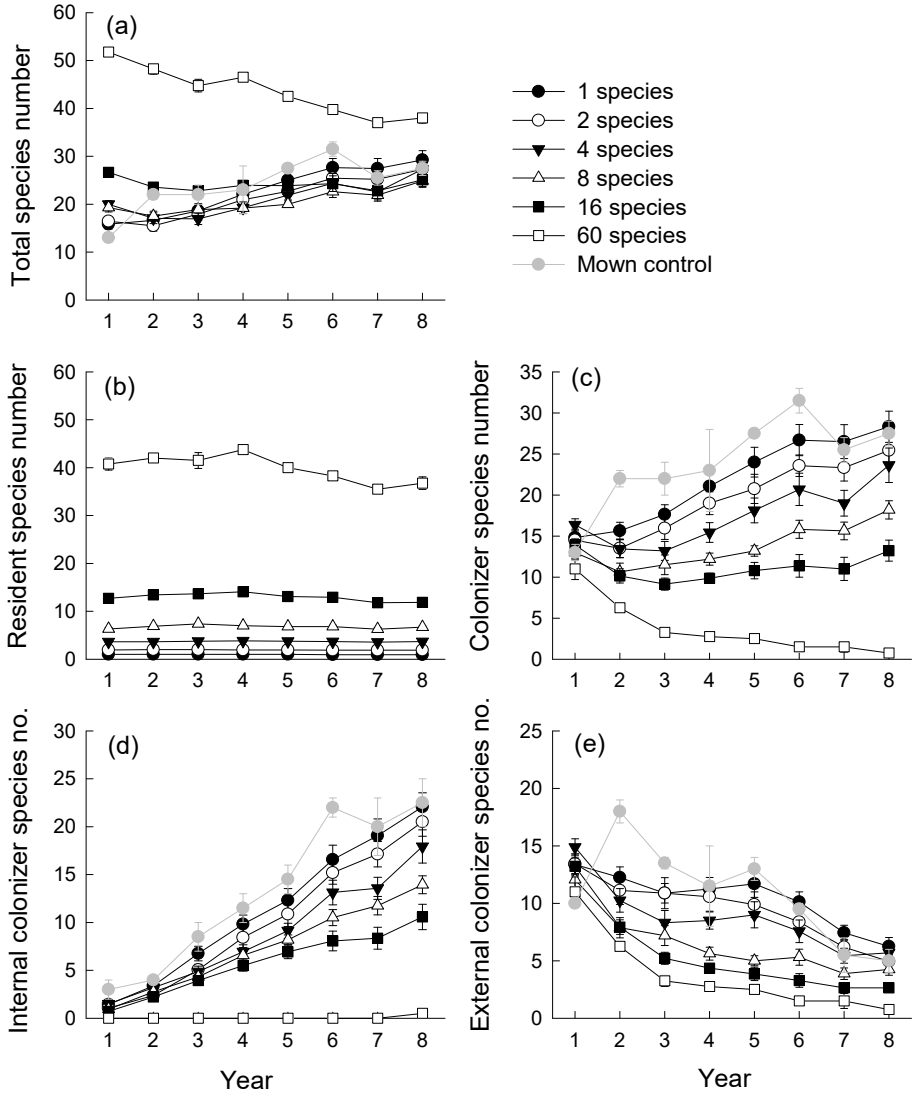
848 Figure 2



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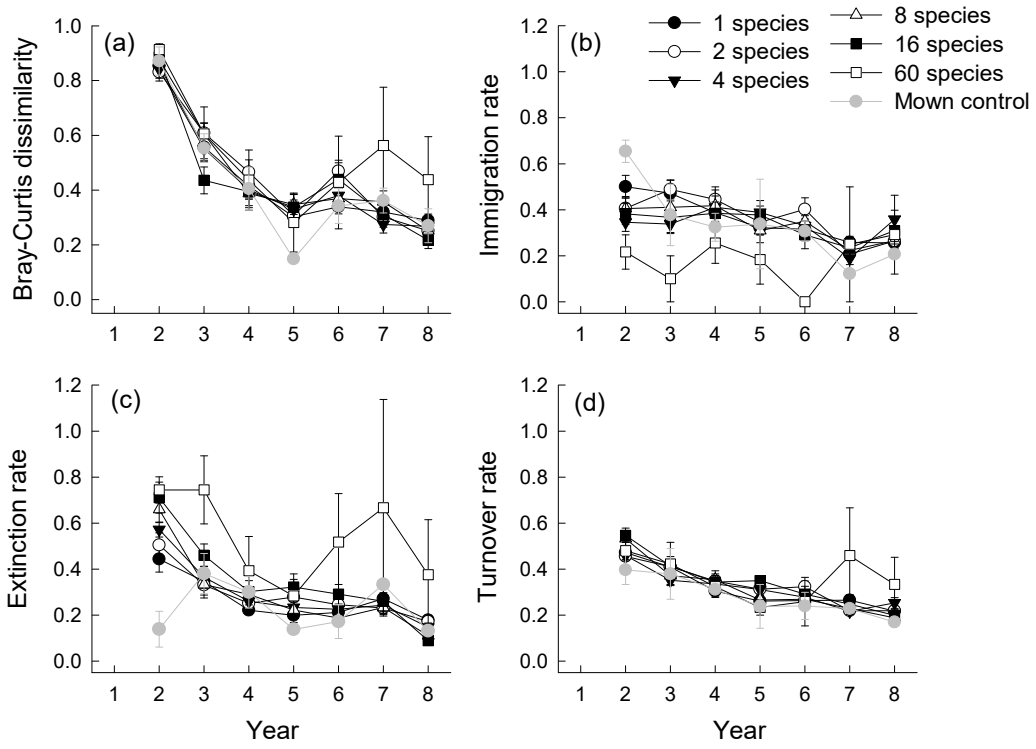
850 Figure 3



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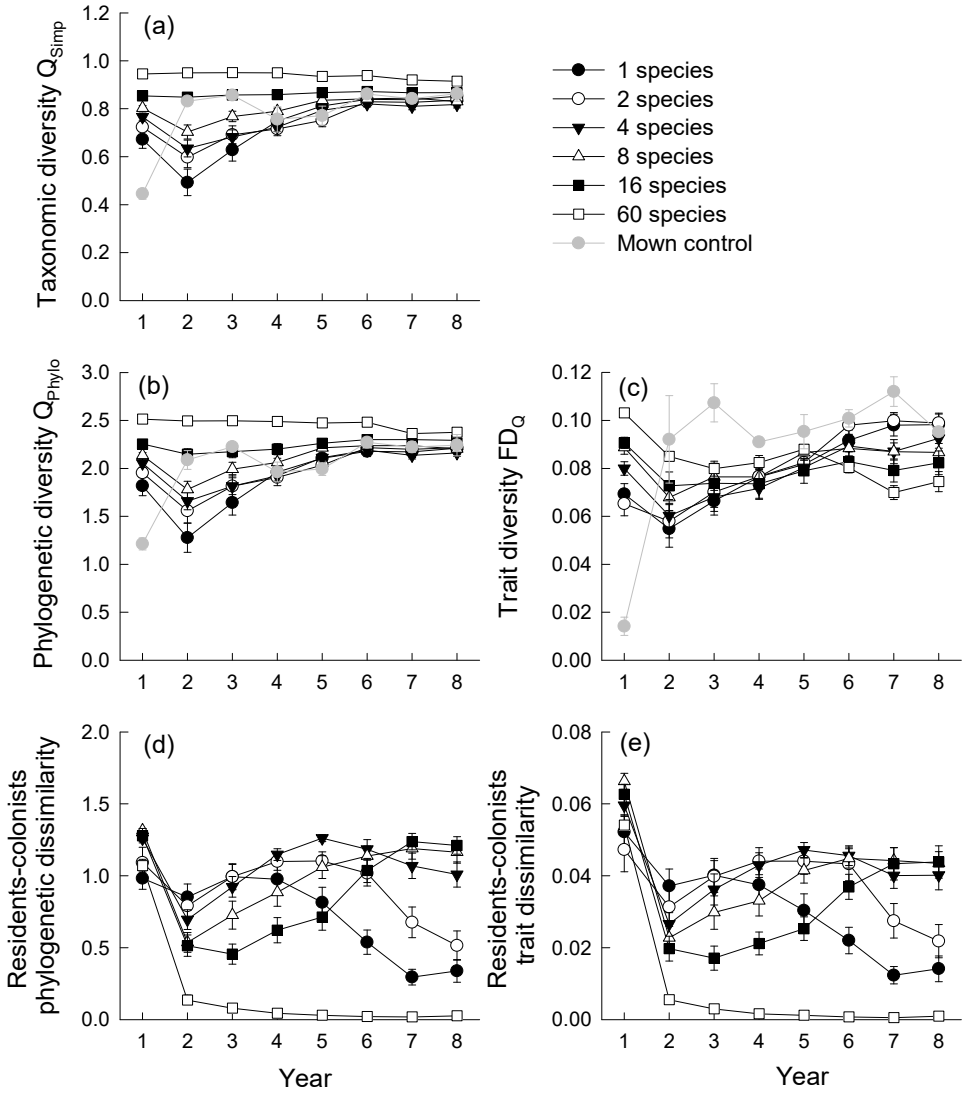

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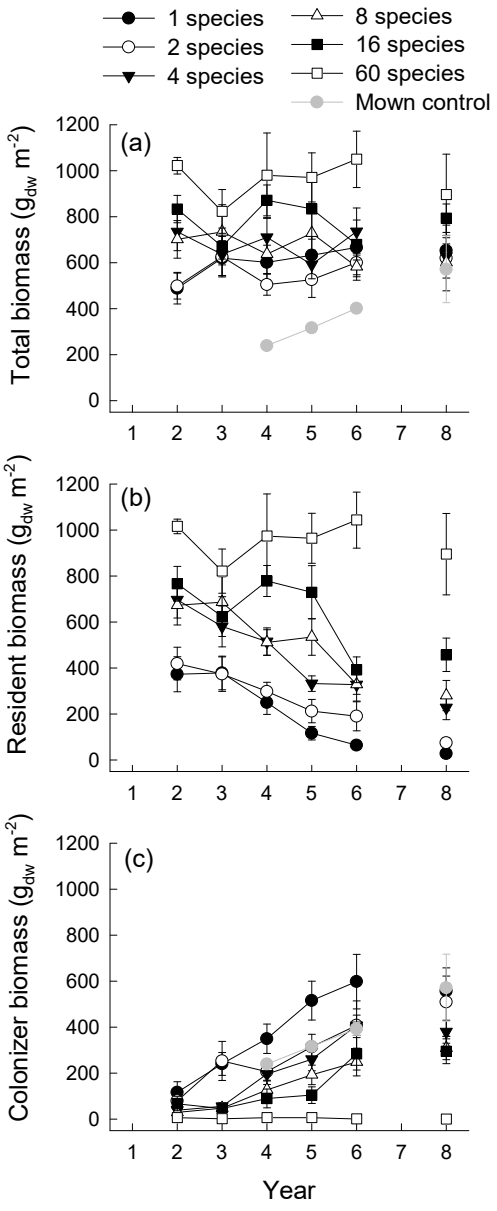
854 Figure 5



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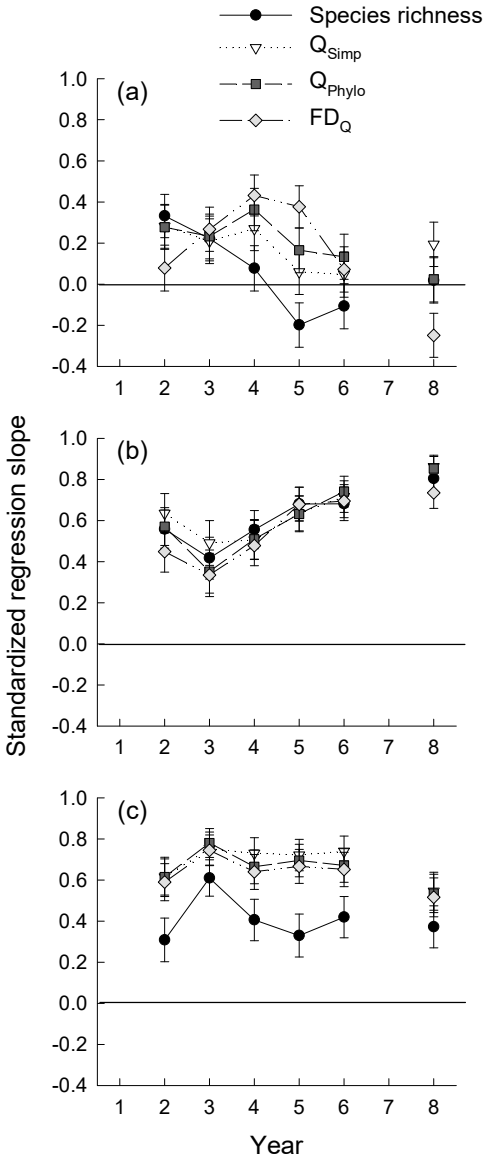
856 Figure 6



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859 Fig. 7

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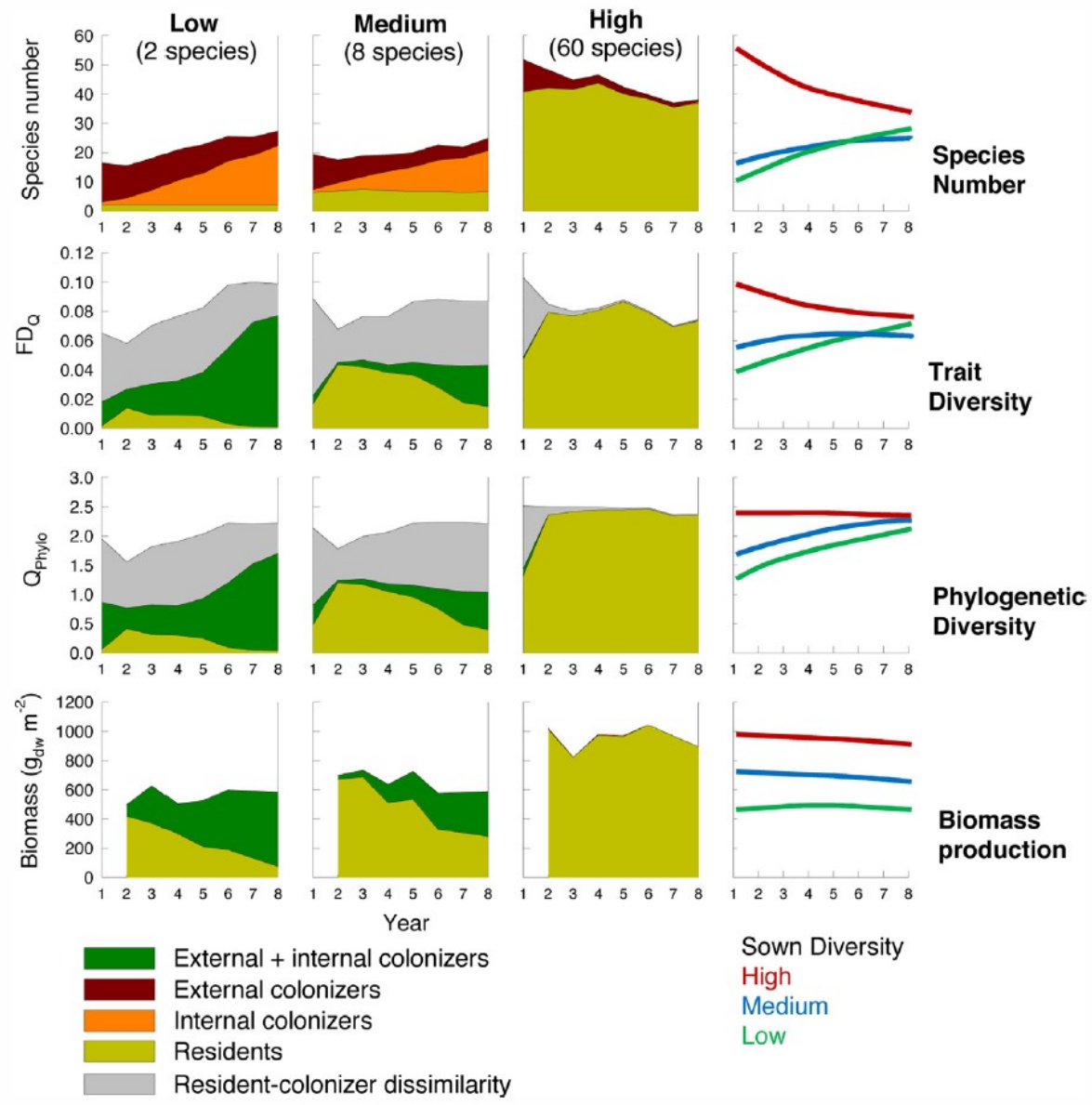

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